THE MECHANICS OF FLIGHT MOVEMENTS IN DIPTERA [1]

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Although the muscles that move the wings in flies and certain other insect groups are activated by the central nervous system, the individual wing movements are not. The wing rate is determined by the load on the flight muscles and was found to bear no relation to the action potentials in these muscles (Pringle, 1949; Roeder, 1951). Two theories have recently been proposed to explain the peripheral control of wing rate in flies. According to Pringle (1949) nerve impulses produce an alteration in the flight muscles so they may be excited on being stretched. By means of the thoracic skeletal connections between them, the shortening of one set of muscles stretches, and so excites, the antagonistic muscles. Boettiger and Furshpan (1950) considered the antagonistic muscles to be under constant tetanic stimulation during flight, the mechanical action at the articulation altering the muscle load so as to produce the oscillation. Both theories suggest that the mechanical action of the thorax controls the physiological response of the muscle.

In spite of the considerable morphological work on the thorax of the fly, relatively little attention has been given to the movements of the articulation induced by the contraction of the large indirect flight muscles. The studies of Lowne (1893) and of Ritter (1911) on the blowfly are the most complete. Mihalyi (1935/36), studying the house fly, has extended the interpretations of Lowne and Ritter to include a more accurate description of some of the mechanical features of the thorax and their relation to flight.

Although Lowne (1893) gives the most detailed description of the articulating structures, in several important aspects his interpretation of their action was in error, for his methods did not show how the parts changed position during flight. The study of living flies treated with CCl_4 has revealed these movements of the articulation and enabled us to obtain a better understanding of flight mechanics. No attempt is made here to produce a complete morphological study. Most of the structures discussed are illustrated in the papers referred to above. Our purpose is to determine how the mechanical features of wing movement are related to the operation of the neuromuscular mechanism.

THE ACTION OF CCL_4

In a short abstract (Boettiger and Furshpan, 1950) the effect of placing flies in CCl_4 fumes was described. There are first violent muscular spasms involving the whole body, with an apparent stiffening of the thorax. Usually anaesthetic flight, a well recognized phenomenon in certain insects, appears. With increasing

action of the CCl_4, the flight tone (wing frequency) increases; then it becomes lower and irregular.   Suddenly the wings stop in either the up or down position, usually the up position.   That this abrupt stop is due to a mechanical inhibition to movement can be shown quite readily.   If the fly is immediately removed from the CCl_4 and the wings moved toward the horizontal position, they will be pushed beyond the catch and will start to beat normally again.   After longer exposures, normal movements will not start when the wings are depressed.   Instead, when a critical point is reached, the wings will click without further effort into the opposite position and remain locked.   In this movement the wings essentially follow the normal flight path with proper changes in angle of attack, indicating that the articulation is set by CCl_4 in the same manner as in normal flight.   The most effective way to move the wings down from the up position is by pressure upon the scutellum.   Pressure upon the posterior lateral region of the scutum will click the wings up.   Small movements of the scutellum in a fly under CCl_4 will produce much larger movements of the wings than rather extensive squeezing of the thorax of an untreated fly.

Evidence was presented (Boettiger and Furshpan, 1951) that this click phenomenon is part of normal flight, and so the action of CCl_4 becomes a new tool for studying the mechanics of flight.   The wings can be frozen in the up or down position and the relations of the parts studied.   Furthermore one can click the wings up and down, thus revealing the dynamic aspects of the mechanism.

All observations reported here have been made on the large flesh fly, *Sarcophaga bullata* Parker.   Other species of Diptera studied gave the same response to CCl_4, but the anatomical details of their articulations have not been investigated.

The Action of the Principal Parts of the Flight Mechanism

The scutellar lever and the action of the indirect muscles

The dramatic movement of the wings produced by pressure on the scutellum of a fly whose wing articulations are set with CCl_4 depends upon the action of the scutellar lever illustrated in Figure 1.   This consists of the scutellum (a) and two lateral anteriorly projecting arms (b).   These are strongly attached to the scutellum by the scutellar bridges (s) and the thickened ventral triangular pieces (t) hollowed out for articulation with the postnotum.   The lever rests upon two earlike lateral projections of the postnotum which fit into special grooves (r) to make an articulation allowing rotation.   Between these points the scutellum connects with the postnotum by a flexible membrane.   The attachment of the lever dorsally to the main part of the notum is through the scutoscutellar suture and the thin flexible cuticle (1-h, Fig. 1) along the lateral arms extending to the clefts between the lever arms and the lateral scutum.   The ventral border of each lateral arm is greatly thickened and bears the posterior notal process (not illustrated).   The lateral arm extends to the axillary region on each side as a process (c).   The x-shaped first axillary sclerite (e, Fig. 3C) sits upon this process.   The outer ventral process of this sclerite fits into a special groove (u, Fig. 1C) in which it slides as the axillary sclerite twists on process (c).

The scutellum is so constructed that the movements of the lateral arms are identical.   Damage to the thin cuticle forming the dorsal surface of the scutellum allows the two wings to be manipulated up and down somewhat independently. Flies so treated cannot sustain themselves in free flight.

The arms of this lever were called the great alar apophyses by Lowne (1893) and given equal importance with the anterior notal process (p, Figs. 1 and 2) in moving the wings.   Ritter (1911) also described the action of the lever arm and termed it the postalaris, the anterior notal process being the prealaris.   The terms
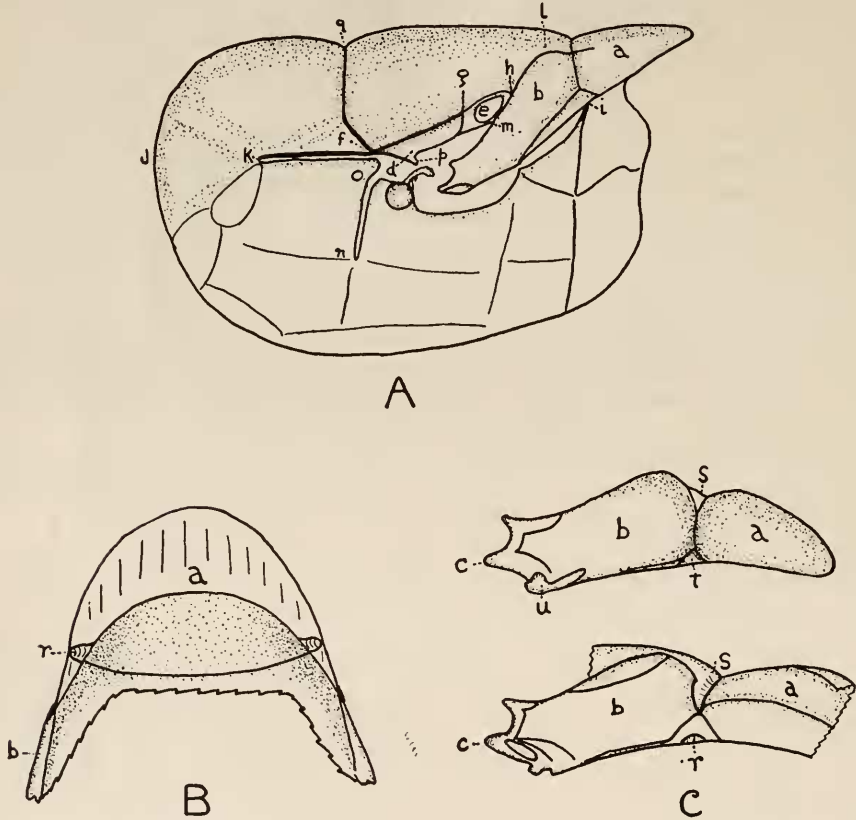

FIGURE 1.   A. Left side of thorax of *Sarcophaga bullata*.   B. Ventral view of scutellar lever dissected free from the thorax.   C. Detail of lever arm and attachment to scutellum, outside above and inside view below.   a, scutellum; b, lever arm; c, process articulating with the first axillary sclerite; d, anterior parascutum; e, posterior parascutum; f, junction of prescutal ridge, transverse ridge and parascutal hinge; g, end of parascutal hinge; h, point in line of attachment of notum with lever arm; i, point of rotation of the scutellar lever on the postnotum; j-k, fulcrum of the notum lever in the action of vertical muscles; l-m, line of attachment of notum with lever arm; n-o, lateral vertical cleft; p, anterior notal process; q, transverse ridge; r, articulating groove for attachment of postnotum; s, scutellar bridge; t, triangular structure supporting articulation of lever and postnotum; u, groove for a process of first axillary sclerite.

anterior and posterior tergal levers were used by Mihalyi (1935/36) who also described the rotation at the junction of notum and postnotum.   These investigators all recognized the opposing action of the anterior notal process and the lever arm. In recent English literature the nomenclature of Snodgrass (1927) has been adopted. He does not describe the action of the lever arm.   Pending some settlement of the

nomenclature by morphologists, the term scutellar lever is used here as it best describes the action of this part of the notum.

The scutellar lever by its simple rotary action and strong construction is designed to transmit the power of the indirect muscles to the wing root sclerites. In the downstroke the longitudinal muscle moves the hinge points (i, Figs. 1 and 2) forward, closing the lateral vertical clefts (n-o, Fig. 1A), while the upward movement of the notum opens the cleft (k-f). Mihalyi (1935/36) first explained the importance of these clefts in allowing proper movement of the thoracic parts. At the same time there is also a lateral expansion of the notum, especially at f (Figs. 1 and 2). The notum rides up and back as the hinge points (i) move forward; the scutellum tips down, and the lever arms move upward. If there is a definite fixed axis on which this rotation occurs, it must lie between points (i) and (1) for (i) moves forward and (1) moves back.

The part played by these structures in the upstroke is as follows. The vertical muscles reverse the rotation produced by the longitudinal muscle. In this action the whole notum anterior to the scutoscutellar suture serves as a lever with fulcrum at j-k (Fig. 1A) and moves the scutellar lever down by action at the attachment
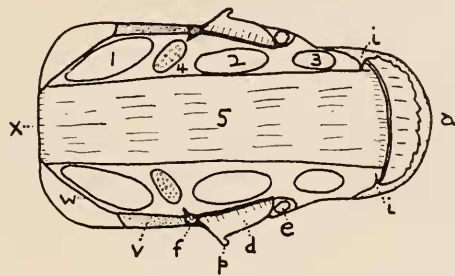

FIGURE 2. Horizontal section through the notum. Structures labeled as in Figure 1 with the following additions: v, prescutal ridge; w, chitinous supporting structure; x, anterior hardened plate; 1, first dorsoventral muscles; 2, second dorsoventral muscles; 3, oblique dorsal muscles; 4, tergal remotor muscles; 5, longitudinal muscles.

line (l-h-m, Fig. 1A). The first dorsoventral muscles shorten very little and move the lever at considerable mechanical disadvantage. They are effective, however, in producing lateral expansion at point f and stiffening the thorax. The second dorsoventral muscles act upon the lever with greater mechanical advantage and may also produce lateral expansion. The oblique muscles attach to the notum just medial to the lever arm at point L (Fig. 1A), and, although they are small muscles, must be quite effective in rotating the lever arms down. The vertical muscles, especially the oblique muscles, are arranged to pull posteriorly as well as downward and so tend to force the hinge points (i) back, opening again the vertical clefts (n-o) without at the same time straining the fulcrum region (j-k).

The generally accepted theory of the production of the up and down movements of the wing suggests that the longitudinal muscles expand the notum laterally on the downstroke, and the vertical muscles draw the notum inward on the upstroke. The recognition of the part played by the scutellar lever eliminates the necessity of assuming this action of the vertical muscles. A study of the insertion of these

muscles on the notum makes it unlikely that they could move the lateral notum inward. In fact Lowne (1893) suggested that the longitudinal and vertical muscles are only partly antagonistic in action, as both tend to produce lateral expansion of the thorax. There must be a continuous outward force produced by the notum and transmitted to the articulation through the anterior notal process. The significance of this force in flight mechanics is discussed in the next section.

The spring mechanism of the anterior notum

The strengthening of certain regions of the thorax was well illustrated by Mihalyi (1935/36), although he does not comment on its significance in flight. Referring to Figures 1 and 2, one can see these structural re-enforcements. Point f is joined to a similar point on the opposite side of the thorax by means of the strong transverse ridge extending over the notum. From f two parallel ridges (prescutal) connected by a stiff membrane (v, Fig. 2) arise and extend anteriorly. A supporting structure (w) connects them with the anterior boundary of the thorax where it joins a hardened plate (x). The transverse and prescutal ridges strengthen the anterior notum so it will resist any force tending to move point f inward.

The attachments of the longitudinal muscle and of the anterior vertical muscles to the anterior notum are so placed that as these muscles shorten, the thorax is put under tension and point f tends to move outward. The thorax and the muscles act together to form a powerful spring. If the outward lateral force produced by this spring is greater than any opposing force, point f, the parascutum (d), and the anterior notal process (p) move outward. As shown below, during the first part of each stroke, an opposing force produced by the scutellar lever moves point f inward, thereby storing potential energy in the spring. At a critical point in the movement of the articulation, this opposing force is suddenly removed. The recoil of the spring completes the movement of the articulation and the wing. The snap action of the scutellum in wingless flies executing flight movements, as previously described by Boettiger and Furshpan (1951), demonstrates the operation of the spring mechanism. The click phenomenon seen in living flies under CCl_4 also results from its action.

The movements of the scutellar lever and of the lateral notum are transferred to the articulating portions of the notum and to the axillary sclerites of the wing base, and thus produce the characteristic pattern of wing movement. The wing cycle then results from the interaction of the anterior parascutum and the anterior notal process, the first and second axillary sclerites, and the mesopleural wing process. Their functions will now be described.

The anterior parascutum and the anterior notal process

The anterior notal process arises, as shown in Figures 1 and 2, from the thickened outer border of a shelf-like structure, formed of the anterior parascutum (d) and the posterior parascutum (e) (terminology of Lowne). Dissecting from the inside, one can see that the anterior parascutum articulates with the main part of the scutum by a concealed hinge (f-g), which allows the shelf to be moved easily up and down. Posteriorly the shelf is connected with the lever arm at h-m. The cleft between the lever and the parascutal shelf, called the tergal cleft by Mihalyi, allows

somewhat independent movement of these two structures, a fact which is important in the production of the basic movement cycle.

As noted above, contraction of either the longitudinal or the vertical muscles will produce lateral expansion of the thorax at point f. This force is transmitted to the articulation by the anterior notal process. In Figure 3 (A and B) the connection between the main part of the notum and the articulation is shown. The existence of the flexible hinge connection (h), not previously described, makes the presently accepted theory of the cause of the down movement of the wings highly
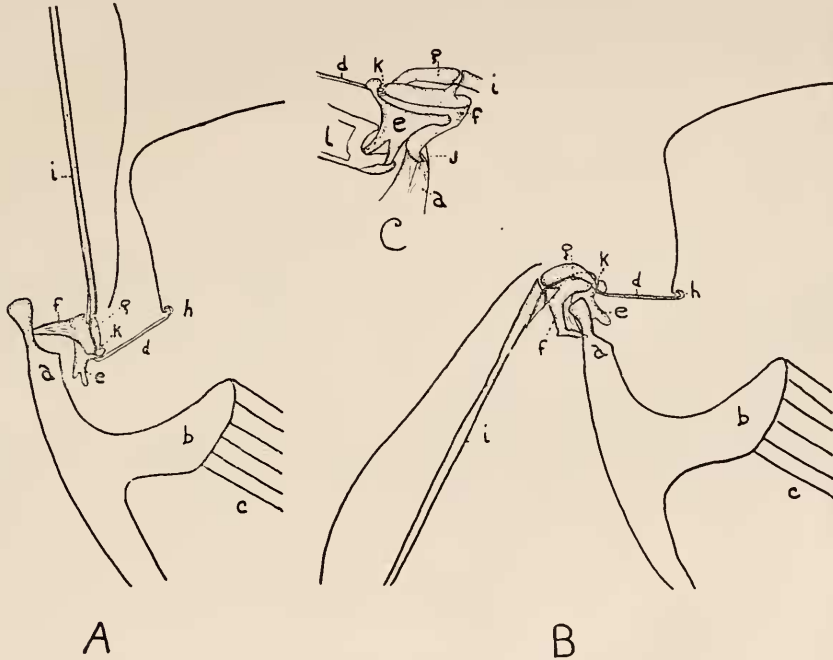

FIGURE 3. Cross sectional view of thorax showing details of the articulation of the right wing. A. Wing in up position, anterior view. B. Wing in the down position, anterior view. C. Posterior view of the axillary sclerites of right wing showing their relation to the mesopleural process, the lever arm and the anterior parascutum. a, mesopleural process; b, pleural apophysis; c, anterior pleurosternal muscle; d, anterior parascutum; e, first axillary sclerite; f, second axillary sclerite; g, base of radial vein; h, hinge; i, radial vein; j, hook articulation; k, point of articulation of anterior notal process, first axillary sclerite, base of radial vein and second axillary sclerite; l, end of the lever arm.

unlikely. Lateral expansion of the notum cannot possibly move the articulation from position shown in Figure 3A to that in Figure 3B as this theory predicts. Expansion of the notum, laterally, would move the hinge outward. However, due to rotation occurring at the hinge, the anterior notal process would not be moved out or up and the wing would remain in the up position (see Fig. 3). Through the anterior notal process the lateral force is focused on the wing articulation. The change in direction of this force necessary to wing movement is produced not by alternate flattening and arching of the notum, but by the scutellar lever. The lever

acts upon the anterior notal process partly through the connection between the lever arm and the parascutal shelf (m-h, Fig. 1) and partly through the first axillary sclerite (e, Fig. 3C).

The first axillary sclerite

The transformation of the movements of the lever and the anterior notal process into the complex wing cycle depends upon the action of the first and second axillary sclerites. Figure 3 (B and C) shows the relationships of the sclerites when the wings are down. The lever exerts its main effect upon the articulation through the first axillary sclerite. The large inner dorsal process of this sclerite hooks into the anterior notal process at k so that as the lever moves up and down, both k and the parascutal shelf are also moved. The second axillary lies between the two dorsal arms of the first axillary. The movement of the second axillary is largely determined by the first axillary.

The second axillary sclerite and the mesopleural wing process

Lowne (1893) described the relation between the second axillary and the mesopleural process in the blowfly. He stated that it is difficult to assign any function to this relation. Ritter (1911) believed the second axillary strengthened the joint by tying together the upper and lower parts. Snodgrass (1927) noted that the second axillary sclerite usually articulates at the side of the mesopleural process, but did not discuss the implications of this fact.

The second axillary is hooked to the side of the mesopleural process (Fig. 3C) and does not disarticulate as suggested by Lowne. The connection is a very strong one and acts almost as a universal joint to allow the complex wing cycle. The second axillary, through its relation to the radial vein, plays an important role in directing the wing. As shown in Figure 3, the base of the radial vein (g) articulates at k along with the anterior notal process and the first axillary. It also makes secondary membranous connections with the second axillary so that rotation of this sclerite moves the wings up and down.

The relation of the base of the radial vein to the second axillary is controlled in part by the direct muscles that fold the wing back over the body and bring it forward into flight position. As the wing folds back the base rotates forward. This arrangement allows some folding of the wing during flight without essentially disturbing the second axillary, the position of which plays an important role in the basic movement of the wing.

As noted above the outward force produced by the notum is transmitted to point k by the anterior notal process. This is opposed by the contraction of the anterior pleurosternal muscle (c, Fig. 3), which is one of the direct flight muscles. As this muscle draws the mesopleural process inward, a force is transmitted to articulating point k by the second axillary sclerite. The inward movement of the mesopleural process is of prime importance in setting the articulation for flight. It occurs in CCl_4-treated flies and is necessary for the production of the click phenomenon.

The position of the mesopleural process determines the range of movement of the lever arm. This is why the movements of the wings of CCl_4-treated flies are more extensive than those of untreated flies. The two lateral arms of the scutellar

lever must move the same for they are strongly connected through the scutellum. Therefore it is important that the muscles exert equal forces on the two mesopleural processes. A provision for this appears to be present. The pleurosternal muscles have a common origin on the flexible sternal apophysis and they tend to act as a single muscle, the ends of which are attached to the two mesopleural processes.

The mesopleural process with its articulating second axillary sclerite opposes the lateral notum with its hinge-attached parascutum. When these structures are properly set by the action of the indirect muscles and the appropriate direct muscles, the basic movement cycle can be produced by the action of the scutellar lever. It is the action of these structures that controls the loading of the fibrillar muscles and makes possible the fast flight movements.

The Production of the Basic Flight Movements

Two conditions are required for the production of the basic flight movements: (1) the activation of the spring mechanism by tension in the indirect muscles, and (2) the inward movement of the mesopleural processes. At the beginning of flight, forces are developed to move the hook articulation of the second axillary inward, and the hinge of the parascutum, which is attached to point f, outward. In a resting fly, point k, Figure 3, is above a line connecting the hinge and the hook articulation. Consequently, as these structures approach one another, point k will move up and the wings down. Records of movements of the scutellum show that in a typical start, a small down movement, which is relatively slow, occurs first. Then the wings are suddenly and rapidly brought up. Subsequent movements occur at a frequency normal for the wing load. The flight mechanism requires a starter, and it is probable that the initial fast up movement is caused by the tergal remotor (4, Fig. 2). This muscle is a vertical muscle but is not fibrillar in structure and responds as normal tubular muscles do.

The positions of the articulating elements when the wings are in the up position are shown in Figure 3A. As the longitudinal muscle shortens, the scutellar lever moves the first axillary sclerite (e) upward. This acts on point k, which can move up only if the mesopleural process and the parascutal hinge are forced apart. By this means, potential energy is stored in the spring mechanism, to be released when point k rises above a line connecting the hook articulation and the hinge. This occurs at the critical point. The recoil of the spring drives the wings down and the articulation into the position shown in Figure 3B. On the up movement of the wings the scutellar lever brings point k down. Again energy is stored in the spring mechanism and released at a critical point.

The critical point on the downstroke occurs when point k rises above the line of force between the hook process and the hinge and on the upstroke when point k moves below this line. Referring to the discussion of the action of the indirect muscles and the movement of the notum, it can be seen that the parascutal hinge must move up on the downstroke and down on the upstroke. This movement alters the position of the line of force between the hook and the hinge. The critical point therefore is at different wing positions on the up and down strokes. The elastic recoil force takes over at least part of the muscle load before the midpoint (resting length of the muscle) is reached.

At the critical point during the movement, the recoil force is maximum, but the major component of the force is not directed to produce rotation of the second axillary. As the movement continues, however, a greater and greater component of the recoil force is in the direction of rotation, while at the same time the force is becoming progressively less as the elastic energy is used up. Vertebrates in their skeletal movements make use of this same mechanical principle (Elftman, 1941).

In flies under CCl_4 an excessive force is produced by the direct muscles (and perhaps the indirect muscles). The indirect muscles are unable to overcome the force and the wings stop in one of the two stable positions, up or down. A similar condition results from high frequency stimulation of the ganglion (Boettiger and Furshpan, 1951). The fast stops in tethered flight reported by Boettiger and Furshpan (1950) and Roeder (1951) can be explained in the same way.

THE WING CYCLE

To sustain the fly in free flight, the basic movements just described must initiate a cycle of wing movements aerodynamically designed to generate a propelling force, the magnitude and direction of which are adjustable by the insect. In this action, the indirect muscles, the direct muscles, and the structural features of the thorax are all concerned. Several authors have concluded, from the histological difference between the direct and indirect muscles, that the direct muscles cannot produce the rapid phasic changes of a single cycle. The observation that the wings of CCl_4-treated flies can be moved through a cycle by simply moving the scutellum is additional eviden for this idea, as no adjustment of direct muscle tension is possible during this m ement. Mihalyi (1935/36) suggested that the indirect muscles, through the special arrangement of the three main articulating structures, can produce the complex wing cycle of straight level flight. He lists these structures as the mesopleural process, the anterior notal process and the lever arm process. The relative movements of these structures determine the movements of the axillary sclerites. These movements are able to produce a normal cycle, however, only when the articulation is set by the action of both the direct and indirect muscles.

The base of the radial vein of the wing is locked into the joint at k, Figure 3A, along with the first axillary and the anterior notal process. The important second axillary, although not articulated at k, is closely tied to this point and to the first axillary. The movements of point k govern the wing cycle. Through secondary membranous connections with the plate-like part of the second axillary, the wing moves with the rotation of this sclerite produced by the movement of k. Point k can move in the three directions, up and down with the lever, forward and back with the anterior notal process, and in and out with the rotation of the parascutum and the movement of the lateral notum.

Referring to Figure 3, one can analyze to some extent the movements that produce the wing cycle. When the wing is in the down position, it is held at the extreme forward point of the cycle in a vertical plane along side of the thorax. The articulation in this condition is shown in Figure 3 (B and C). As the vertical indirect muscles shorten, the scutellar lever process (1, Fig. 3C) starts to move down. The parascutum (d) does not move much at first, as it is held by the tension between the mesopleural process (a) and the parascutal hinge (h). Therefore, the second axillary first tips back, rotating the base of the wing so as to raise the an-

terior margin and depress the membranous part. As the lever continues to move down, point k moves more rapidly. The wing flips up and back in an effective stroke with the anterior margin of the wing leading. Before coming into the up position, a rotation of the wing base depresses somewhat the anterior wing margin. This is shown by the fact that in CCl_4-treated flies the wing locks into the up position with the anterior margin of the wing leading in a position to begin the downstroke. This rotation during the upstroke is due to the forward movement of point k, produced by the anterior notal process, and the twisting of the second axillary, resulting from the inward and downward movement of the lever arm.

The downward movement of the wing is also initiated by the scutellar lever as it is moved up by the shortening of the longitudinal muscles. The first axillary is lifted in such a way that the second axillary twists to tip the anterior margin of the wing down. Then point k flips up and the wing, held at the proper angle of attack, moves down. During the down stroke, the backward movement of point k and the forward movement of the lever arm process twist the second axillary, thereby insuring the full forward sweep of the wings. In CCl_4-treated flies the wing locks in the down position with the anterior margin closer to the body than the membranous portion as shown in Figure 3B. The wing is set as at the end of a downstroke, instead of ready for the upstroke. At the beginning of the upstroke the anterior margin of the wing must be raised while the membranous portion is depressed, as noted above. The upstroke is more complicated. The articulation is set to raise the anterior margin of the wing at the beginning of the upstroke and depress it at the end. Records of movements of the scutellum during a quick stop reveal a basic asymmetry in the articulation. In a quick stop on the downstroke there is some movement of the scutellum before the stop point is reached. On the upstroke the stop occurs almost at the extreme down position of the scutellum (Boettiger and Furshpan, unpublished).

The base of the wing makes secondary connections to the driving mechanism. The most important one is with the posterior notal process, which arises from the ventral border of the scutellar lever arm. This undoubtedly aids in tipping the wing and supporting the base against the effects of air pressure. However, cutting the posterior notal processes on both sides does not destroy the fly's ability to maintain itself in free flight.

The Mechanical Limits to Movement

Normally, more energy is released than is necessary to complete the movement (Boettiger and Furshpan, 1951). The freely moving lever is stopped by definite mechanical limits, which appear, however, to have some elasticity. The kinetic energy of the moving wings may be partially recovered by this means, as suggested by Chadwick (1951). The lever arm can move down without hindrance until its ventral ridge contacts the pleural sclerites. This first occurs quite near to point i (Fig. 1), as the arm is set at an angle so that it moves inward as it moves down. The second axillary sclerite seems to limit the up movement of the lever. As the lever pushes against the first axillary, the second axillary moves into the position shown in Figure 3C. The hook articulation with the mesopleural process prevents any further upward movement of the second axillary and hence of the first axillary and the lever. The presence of mechanical stops may increase the effi-

ciency of the mechanism by eliminating the necessity for doing negative work in stopping each movement (Fenn, 1930).

THE STEERING MECHANISM AND THE CONTROL OF AMPLITUDE

The movements of the lever arms and therefore of the articulation must have the same amplitude on the two sides. The construction of the scutellum does not allow one arm to move more than the other. If the wings are not drawn forward into flight position when a fly is under CCl_4, the amplitude of the wing movement when the scutellum is depressed is quite small. Even though the wings merely tip down, the click action is present and the lever arms move the full limit. The first axillary does not twist outward and forward as it does on the downstroke when the wings go through their full amplitude. As the wings are brought forward by direct muscles, the amplitude increases. Frequently, mounted flies will show erratic movements and hold one wing back while the other moves with normal amplitude. They spin around toward the side of the smaller movement. In a similar manner, a free flying insect can alter its direction without changing the action of the indirect muscles or of the scutellar lever. Should the fly wish to rise or fall, the tension in the proper direct muscles is adjusted, altering the wing cycle equally on both sides and again requiring no change in the driving mechanism.

Chadwick and Williams (1949) and Chadwick (1951) have made a quantitative study of wing movements in Drosophila at various air densities. Reducing the density of the air lowers the wing load and increases both frequency and amplitude. The increase in frequency is proportional to the increase in amplitude. This proportionality may be interpreted to mean that the increased amplitude observed at low air density is the result of the greater momentum of the faster moving wings. With greater momentum the articulation moves further into the elastic mechanical stop. In addition, each wing will also bend more when its articulation is suddenly stopped and this would be recorded as an increase in amplitude. Changes in frequency and amplitude may, therefore, be produced experimentally without alteration in the action of the basic neuromuscular mechanism. Roeder (1951) has found that reducing muscle load by removal of the wings results in a decrease in frequency of thoracic potentials. This suggests that receptors, responsive to wing load, can exert some control over the indirect flight muscles.

The amplitude of wing movement must be controlled to some degree by the central nervous system. In the first place, the wings may be held forward or back as described above so that their amplitude is large or small. Secondly, the tension between the mesopleural process and the parascutal hinge which determines the spring action of the notum can control wing amplitude. If this tension is large, the indirect muscles must, in overcoming this force, store a great amount of energy in the spring mechanism. The recoil action will then throw the articulation to the limit and so give maximum wing movement. On the other hand, if the tension is small, less energy is stored and the recoil may not move the articulation to its limit. In a normal stop there is a progressive decrease in amplitude of wing and articulation. This is apparently due to the relaxation of the direct muscles controlling the position of the mesopleural processes. Records show that during continuous flight under constant conditions, the amplitude of movements of the scutellar lever is remarkably uniform. Occasional changs in amplitude may be accounted for by al-

tered tension between the mesopleural process and the parascutal hinge. The indirect muscles by controlling the spring action of the notum may contribute to these amplitude changes.

SUMMARY

1. The mechanics of insect flight are usually studied by squeezing the thorax so as to imitate the action of the indirect flight muscles. In flies certain elements of the articulation are not properly set in such experiments, so the interpretations made are not accurate. That CCl_4 sets the articulations of flies as in normal flight is shown by the dramatic wing movements easily produced in these insects. This report is based on the study of CCl_4-treated flies and outlines the main features of the mechanics of wing movement. Much additional physiological evidence for the interpretations given here has been accumulated and will be reported separately. The abstracts referred to state some of the experimental results.

2. The secret of the peripheral control of wing rate certainly lies in the indirect flight muscles. These muscles are the power plants of the wings, operating in essentially an all-or-none fashion. It is shown here that they play little part in steering or in amplitude changes. They operate between definite mechanical limits and so do not halt each other's movement as in a conventional antagonistic system.

3. The anterior notum is shown to have a spring action which unloads the muscle at a critical point and so plays a basic physiological role. If the recoil of the notum alone is capable of completing the movement, the indirect flight muscles would not be required to exert any tension at their resting or shorter lengths. The energy would be put into the mechanism almost isometrically and it would not be necessary to assume high tension in a rapidly shortening muscle.

4. By a combination of the mechanical properties of the thorax and the physiological properties of the fibrillar muscle the peripheral control of wing rate is achieved.

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